

TERTIARY OCCURRENCE OF THE FERN *LYGODIUM* (SCHIZAEACEAE) IN AUSTRALIA AND NEW ZEALAND

A.C. ROZEFELDS, D.C. CHRISTOPHEL AND N.F. ALLEY

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Lygodium is ubiquitous in early Tertiary floras of Australia. Sterile and fertile leaves of the climbing fern *Lygodium* are found in Eocene deposits from Anglesea (Victoria), Maslin Bay and Golden Grove (South Australia) and in the early Tertiary from Dinmore in Queensland (*L. dimorphyllum* Churchill, 1969). Sterile material is known from Late Eocene/Early Oligocene sediments at Cethana (Tasmania) and the Middle Eocene at Temuka, in New Zealand.

New material from the Golden Grove, Maslin Bay and Anglesea localities including sterile and fertile pinnules, spores, and cuticular structure is referred to *L. dimorphyllum*. The fertile pinnules contain spores of *Cyathidites splendens* Harris, 1965. This palynomorph has a Late Cretaceous (Maastrichtian) to Pliocene range in southern Australia. The Australian species is very similar to the Eocene Chilean *L. skottsbergii* Halle, 1940, in sterile and fertile pinnule morphology. Heterophylly presents problems in interpreting variation in fossil *Lygodium*. □ *Lygodium*, *Schizaeaceae*, *Cyathidites splendens*, *Tertiary*, *palynology*, *palaeobotany*, *biogeography*, *Australia*, *New Zealand*.

Andrew C. Rozefelds, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; present address: School of Botany, University of Melbourne, Parkville 3052, Victoria, Australia; D. C. Christophel, Botany Department, University of Adelaide, PO Box 496, Adelaide 5001, South Australia, Australia; N. F. Alley, South Australian Department of Mines and Energy, PO Box 151, Eastwood 5053, South Australia, Australia; 25 June, 1991.

Extant *Lygodium* is a pantropical climbing fern with temperate outliers occurring in New Zealand (*L. articulatum* A. Rich.), eastern United States (*L. palmatum* (Bernh.) Swartz and Japan [*L. japonicum* (Thunb.) Sw.]. About 40 species are known world wide with four occurring in Australia (Holtum, 1959). The Australian species *L. japonicum* (Thunb.) Sw., *L. flexuosum* (L.) Sw., *L. microphyllum* (Cav.) R. Br. and *L. reticulatum* Schkuhr are tropical occurring in northern and eastern Australia. In this paper, fossil *Lygodium* leaves including sterile and fertile pinnules are described from Dinmore (Queensland), Maslin Bay and Golden Grove (South Australia) and Anglesea (Victoria) and a number of other localities in southern Australia and New Zealand (Fig. 1). Previous records of *Lygodium* or *Lygodium*-like ferns are reviewed. Problems inherent in classifying and describing variable taxa are discussed.

PREVIOUS RECORDS OF FOSSIL *LYGODIUM* IN AUSTRALIA AND NEW ZEALAND

Lygodium or *Lygodium*-like fossils have been reported by Johnston (1894), Ettingshausen (1886, 1888), Shirley (1898), Churchill (1969),

Hill et al. (1970), Douglas (1978), Peters & Christophel (1978) and Christophel & Greenwood (1987). Churchill's material was the first unequivocal fossil evidence of the genus in Australia. The taxa described in the 19th century were based on fragmentary sterile pinnules but none can be confidently assigned to *Lygodium* (Churchill, 1969). Of these taxa the type of *Osmunda tasmanica* Johnston from Glenora, could not be located in collections in Tasmania (R. S. Hill & N. Kemp, pers. comm.). The holotype of *L. strzeleckii* Ettingshausen, 1886, collected from the Vegetable Creek locality was restudied and prepared further (Fig. 3A) but referral to *Lygodium* is dubious because it is based upon small pinnule fragments with abraded margins. The Late Triassic *Lygodium antiquorum* Shirley, 1898 from the Ipswich Coal Measures is based upon a trilobate seed fern or fern pinnule (Fig. 3F) with no evidence of sporangia, and is not referable to *Lygodium* as Walkom (1917) indicated.

Churchill (1969) described *L. dimorphyllum* based upon two fertile pinnules from the early Tertiary Redbank Plains Formation at Dinmore in south eastern Queensland. Hill et al. (1970) recorded sterile *Lygodium* pinnules from Dinmore, which they referred to *L. skottsbergii*. Douglas (1978) figured a fertile *Lygodium* pinna

from Anglesea in Victoria. A fern frond tentatively compared with *Lygodium* has also been figured from the Cenomanian Winton flora of Western Queensland (Peters & Christophel, 1978). Christophel & Greenwood (1987) recorded *Lygodium* from the Golden Grove locality.

Additional material was collected from Dinmore and Anglesea by ACR and DCC respectively over a number of years. *Lygodium* has also been recently collected from the Middle Eocene Maslin Bay and Golden Grove floras (South Australia) and the Late Eocene/Early Oligocene Cethana flora of Tasmania (R. Carpenter, pers. comm.). *Lygodium* pinnae have also been recognized from Temuka in New Zealand (D. Mildenhall, pers. comm. 1986).

LOCATION OF SITES AND AGES OF FLORAS

The Dinmore site in the Redbank Plains Forma-

tion, south eastern Queensland is of Paleocene/Eocene age (Day et al., 1983). This largely undocumented flora includes ferns, Podocarpaceae and dicotyledonous leaves (Hill et al., 1970; Selling, 1950).

The diverse Anglesea flora occurs in the Middle Eocene Eastern View Coal Measures, and while *Lygodium* occurs in most lenses the majority come from the *Gymnostoma* lens (Christophel et al., 1987). Elements of the Maslin Bay flora were described by Blackburn (1981) from a carbonaceous clay lens in the Middle Eocene North Maslin Sands (McGowran et al., 1970; Alley, 1987). A well preserved flora from the North Maslin Sands at Golden Grove, north of Adelaide is also Middle Eocene in age. A recent overview of the flora has been provided by Christophel & Greenwood (1987).

The Late Eocene/Early Oligocene Cethana flora has yielded *Nothofagus* leaves (Hill, 1984), and the remaining flora, which includes 'tropical'

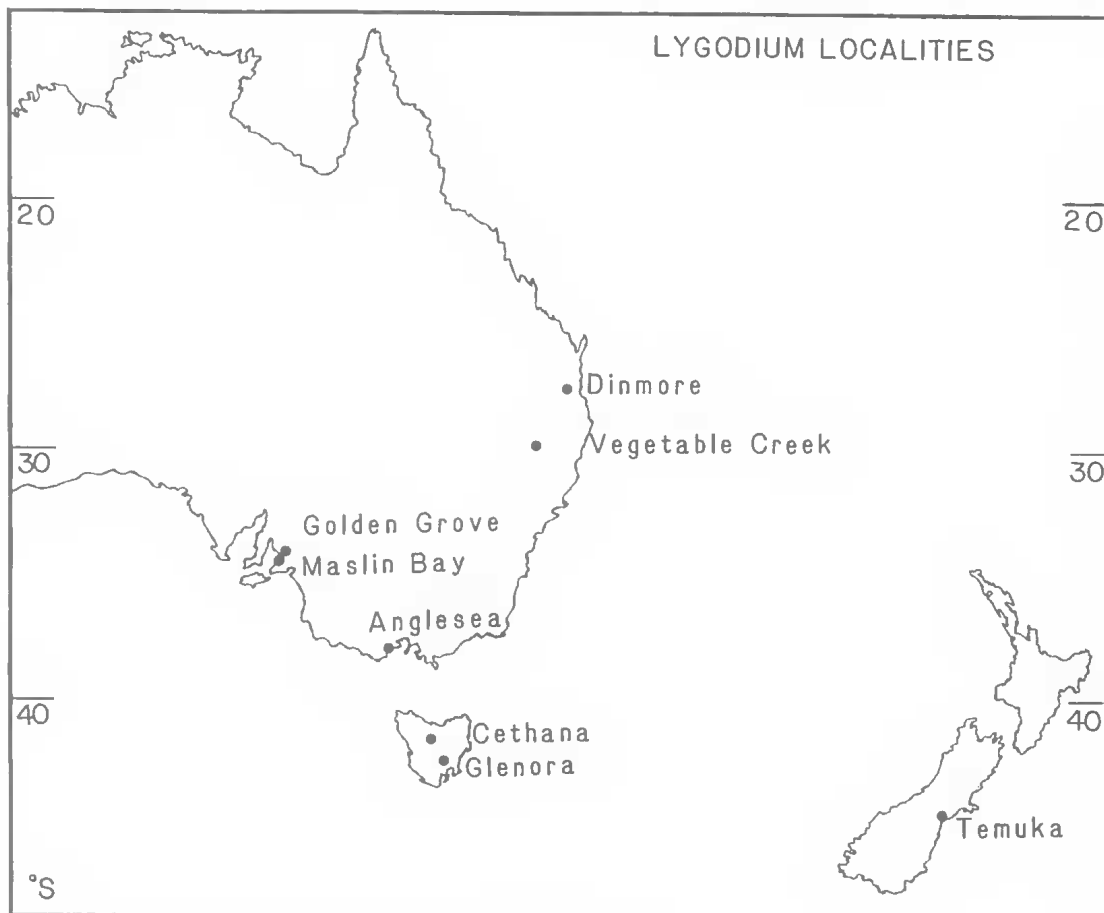


FIG. 1. Fossil *Lygodium* localities in Australia and New Zealand.

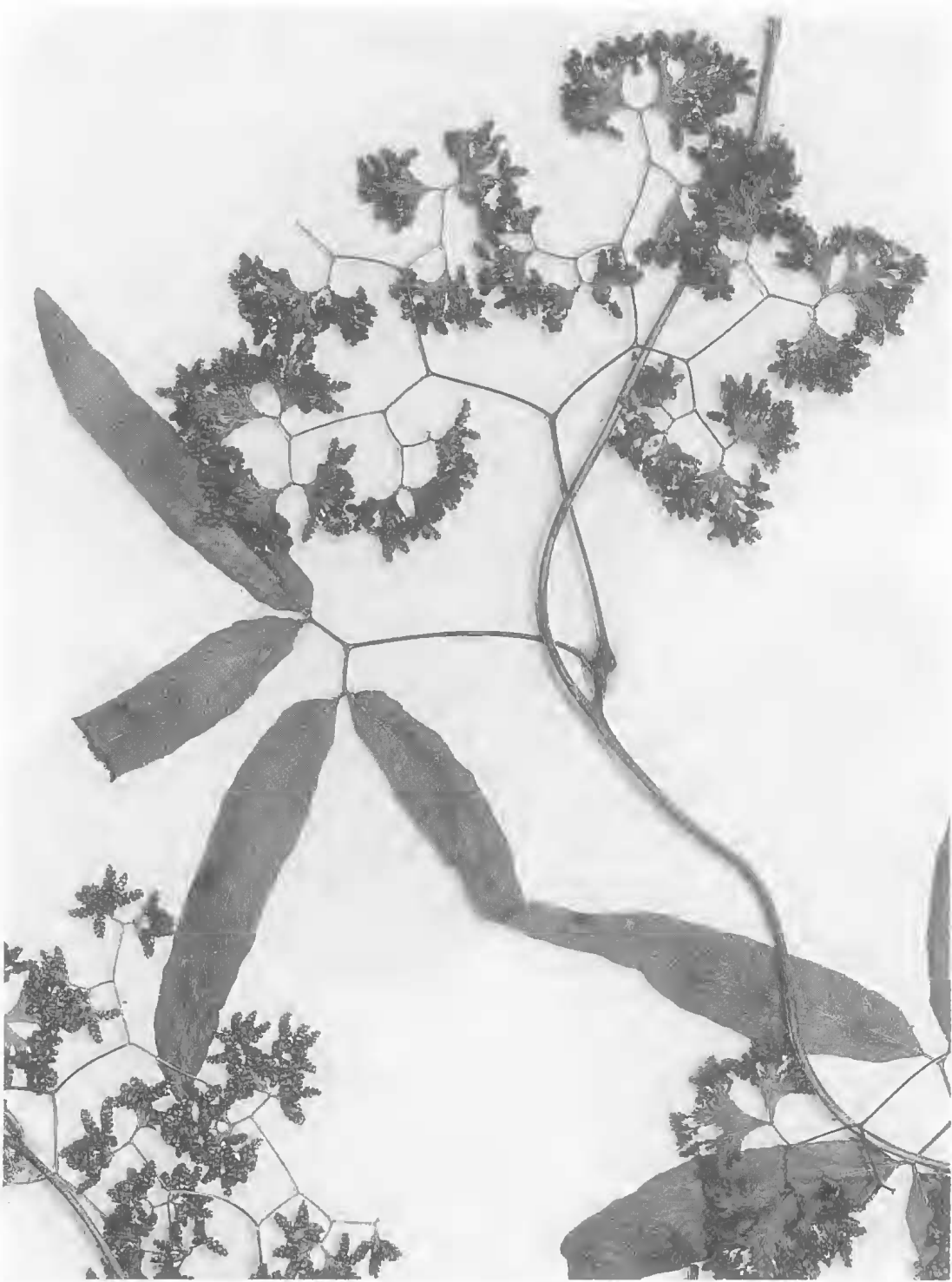


FIG. 2. *Lygodium articulatum* A. Rich. from Fairy Falls Track, Waitakere Range, South of Auckland, New Zealand. DSIR, Christchurch CHR153015. Note abscission nodes at base of sterile pinnules and the varying development of lamina between sorophores. [Photograph supplied by Bryony MacMillan, DSIR, Christchurch, New Zealand].



rainforest elements is presently being studied (R. Carpenter, pers. comm., 1987). The geology and stratigraphic information on the Temuka potteries clay pits in New Zealand indicates an Eocene age for this flora (Wellman, 1953; Gair, 1967). Specimens from these two localities were not available for study.

METHODS AND PRESERVATION OF FOSSILS

The Dinmore, Cethana and Vegetable Creek materials are preserved as impressions in fine grained mudstones lacking cuticle. Latex peels of the surface of sterile *Lygodium* pinnules from Dinmore, examined with a SEM, yielded no cellular information (D. Dilcher, pers. comm.). However, SEM examination of fragments of the original specimen do show some cellular information (Fig. 11A,B). The Maslin Bay and Anglesea specimens are preserved as compressions or impressions while *Lygodium* leaves and sorophores from Golden Grove are 'mummified'. The method for preparing 'mummified' leaves follows that of Christophel (1984). The Golden Grove *Lygodium* leaves are usually opaque and could not be studied using the fluorescence technique of Friedrich & Schaarschmidt (1977). Small areas of venation in these specimens were illuminated using narrow beams of light from cold light sources.

The mummified sorophores and small fragments of leaf cuticle from Golden Grove were cleaned with concentrated HF acid for a few days and the sporangia were gently macerated to release spores. Spores were studied and photographed with a Zeiss Photomicroscope 111. Fragments of cuticle from the sorophores and leaves were washed in distilled water, airdried and sputter coated with platinum. Material was examined with a JEOL JSM 840 scanning electron microscope with lanthanum hexaboride filament at 5kv.

Lygodium examined in this paper (Appendix A) includes material from the Queensland Museum (QMF), Geological Survey of Queensland (GSQF), University of Queensland (UQF), Museum of Victoria (NMVP), University of Tasmania (UTC), University of Adelaide (Maslin Bay, UAS; Golden Grove, UAG), and Geological Survey of New Zealand (GSNZ). Modern

Lygodium material collected by ACR for this study, will be donated to the Queensland Herbarium (BRI).

SYSTEMATIC PALAEOBOTANY

Family SCHIZAEACEAE

Lygodium Sw.

The new *Lygodium* material from the various Australian localities is considered to be conspecific with *L. dinmorphyllum* Churchill from Dinmore in south eastern Queensland. An emended diagnosis of this taxon including information on spores, cuticle and foliar heteromorphism is given, as Churchill's description only covered the gross morphology of the fertile pinnules.

Lygodium dinmorphyllum Churchill, 1969 (Figs 4-10)

1969 *Lygodium dinmorphyllum* Churchill, pp. 257-265, fig. 2.

1970 *Lygodium skottsbergii* Halle, Hill et al., pl. Czll, fig. 1.

EMENDED DIAGNOSIS

Sterile pinnules asymmetrical, usually 2-3 lobed, although unilobate, quadrilobate and pentalobate pinnules occur. Lateral lobes tend to be longer than central lobes. Pinnule base is cuneate to truncate, apex rounded to acute. Pinnules petiole, lacking abscission node at pinnule base. Venation palmate, dichotomously branching from the central vein, on each lobe, two to three times before reaching leaf margin. Leaf length variable, maximum lobe length about 110mm. Pinnule margin variable, undulose in larger specimens, smooth in small pinnae, rarely lobed. Pinnules probably hypostomatic. Anticlinal walls of abaxial epidermis strongly sinuous, stomata anomocytic. Stomatal apparatus 30µm long, (29-32µm) and 27µm wide (25-32µm).

Fertile pinnules in branched axes often lack lamina, although lamina sometimes present as narrow wing or flange at the base of sorophores. Individual sorophores variable in size, ranging

FIG. 3. A. Holotype, *Lygodium strzeleckii* Ettingshausen, from Vegetable Ck, GNSWF8820, $\times 3$. B,C, Cethana ferns. B, fern aff. *Lygodium*, sterile pinnule UTC235. C, Bilobate sterile *Lygodium* pinnule UTC232, $\times 2$. D,E, Temuka *Lygodium*, New Zealand. D, GSNZ25/90, $\times 1.7$. E, GSNZ25/92, $\times 2$. F, Holotype, *Lygodium antiquorum* Shirley, GSQF143, $\times 3.5$. [D, Mildenhall (DSIR, New Zealand Geological Survey, Lower Hutt) and R. Carpenter (University of Tasmania) supplied photographs of the Temuka and Cethana specimens respectively].

from about 4.0-14.0mm in length, often united in groups of 2-4. Spores referable to *Cyathidites splendens* Harris, 1965. Sinuosity of anticlinal walls of epidermis on sorophore lamina not as pronounced as in sterile pinnules.

REMARKS

The Golden Grove and Anglesea localities have yielded *Lygodium* sorophores containing *C. splendens* spores. *C. splendens* is also a common palynomorph in the Maslin Bay palynoflora. While spores have not been isolated from the Dinmore sorophores and the cuticle is poorly known, it seems preferable to refer the new material to *L. dinmorphyllum* than erect a doubtfully distinct taxon. Based upon the widespread distribution of *C. splendens* in the early Tertiary and Late Cretaceous in Australia it seems likely that the Dinmore sorophores also had *C. splendens* spores. *Lygodium dinmorphyllum* is closely comparable with *L. skottsbergii* but is considered distinct based upon spores and cuticular information. Halle (1940: 259) noted that the spores of *L. skottsbergii* are finely punctate or almost smooth and hence differ from *C. splendens*.

The only contra-indication that the *Lygodium* material from Australia may include a number of taxa is the variation in the angle of lower order branching in the fertile axes at different localities. In a relatively complete non-distorted specimen from Anglesea (Fig. 8D), the angle of branching is (130-150°), which is similar to that of modern *L. articulatum* (Fig. 2). The Dinmore material typically has acutely angled lower order branching in the fertile pinnac, i.e. (75-85°) (Fig. 4A, G,H). Relatively complete and undistorted fertile axes have not been collected from Golden Grove or Maslin Bay so the angle of branching in the fertile axes from these localities is unknown. The systematic implications are difficult to assess because insufficient material has been collected from enough localities to assess variation.

FOLIAR HETEROMORPHISM IN EXTANT *LYGODIUM*

Foliar heteromorphism is the production of morphologically variable leaf types on the same individual (Eckenwalder, 1980). Changes in the size and shape of successive leaves can be due to heteroblastic development (Wareing & Phillips, 1982). This may occur in the transition from juvenile to adult leaves or may result from environmental factors. In *Lygodium*, transition from sterile to fertile pinnac results in morphologically distinct pinnac. Pinnac intermediate in character between sterile and fertile pinnules occur in *L. articulatum* and *L. palmatum*. The lamina in the fertile pinnac of the extant species *L. articulatum* and *L. palmatum* is very reduced and the pinnules are strongly dimorphic (Fig. 2; Manchester & Zavada, 1987, figs 9,11). The degree of lamina reduction varies in fertile leaflets of *L. articulatum* (Fig. 2).

In *Lygodium*, there is great plasticity of form in sterile and fertile pinnac, and fusion of pinnules occurs. Sterile leaflets in extant *L. articulatum* are characteristically unilobate although fused bilobate pinnules also occur. Fusion of pinnules may explain some variation in fossil material from Australia.

Aberrant pinnules with accessory lobing were collected from Dinmore, Maslin Bay and Golden Grove (Fig. 9G,H) and were also figured for *L. kaulfussi* Heer, 1861 by Manchester & Zavada (1987). In modern *L. reticulatum* from north eastern Queensland similarly deformed leaves also occur.

FOSSIL *LYGODIUM* MORPHOLOGY

Taxonomic treatments of extant *Lygodium* are based upon the form of sterile and fertile pinnules, spores, venation and mode of branching. Holttum (1959: 39) commented that 'there is so much variation in leaflet form due to the age of the plant,

FIG. 4. Fertile *Lygodium dinmorphyllum* pinnules from Dinmore. A, QMF14465, $\times 1.9$, sporangial head free of lamina. B, QMF14530, $\times 2$, lamina around sporangial heads. C,D, GSQF12973. C, $\times 2.8$. D, $\times 1.0$. E,F, QMF14361. E, $\times 3.1$. F, $\times 1$. G,H, QMF12544. G, $\times 3.3$. H, $\times 1$.

FIG. 5. Sterile *Lygodium dinmorphyllum* pinnules from Dinmore, illustrating variation in pinnules. A, QMF18035. B, QMF15320. C, QMF14365. D, QMF2858. E, QMF15319. F, QMF14974. G, QMF14363. H, UQF32006. I, GSQF12974. J, QMF14366. All natural size.

FIG. 6. Sterile *Lygodium dinmorphyllum* pinnules from Dinmore, illustrating variation. A, QMF 18035, $\times 1$. B, QMF14809, $\times 2$. C, UQF32006, $\times 1.4$. D, QMF14363, $\times 3.5$.

FIG. 7. Fertile and sterile *Lygodium dinmorphyllum* pinnules from Maslin Bay. A,B, Sterile trilobate pinnule, UAS715. A, $\times 2$. B, $\times 1$. C, Fertile pinnule UAS3524, $\times 5$. D,E, Sterile unilobate pinnule with poorly developed secondary lobe, UAS2274. D, $\times 2.3$. E, $\times 1.0$. F,G, Bilobate sterile pinnule, UAS1211. F, $\times 1.9$. G, $\times 1.0$.

Figure 4

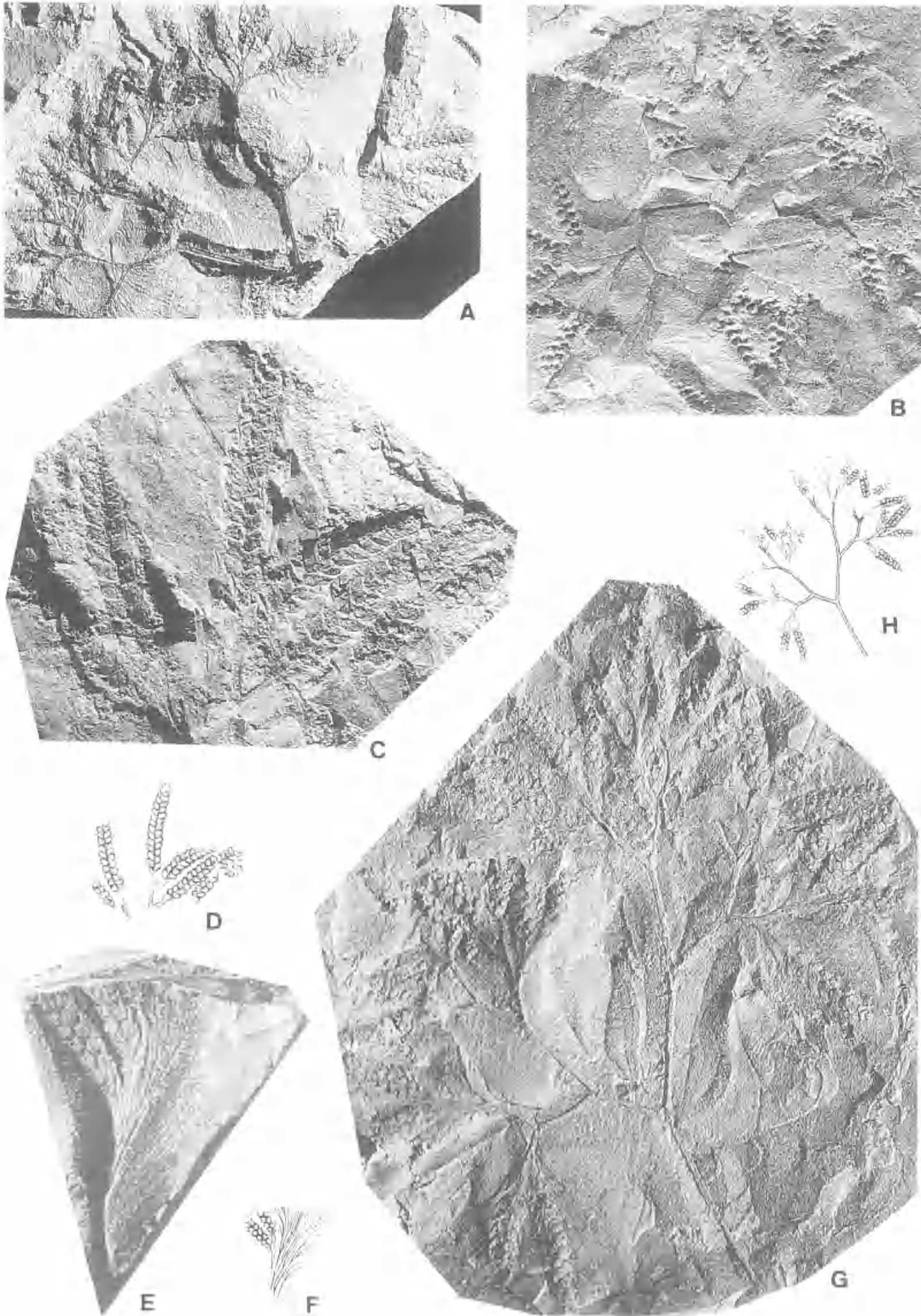


Figure 5

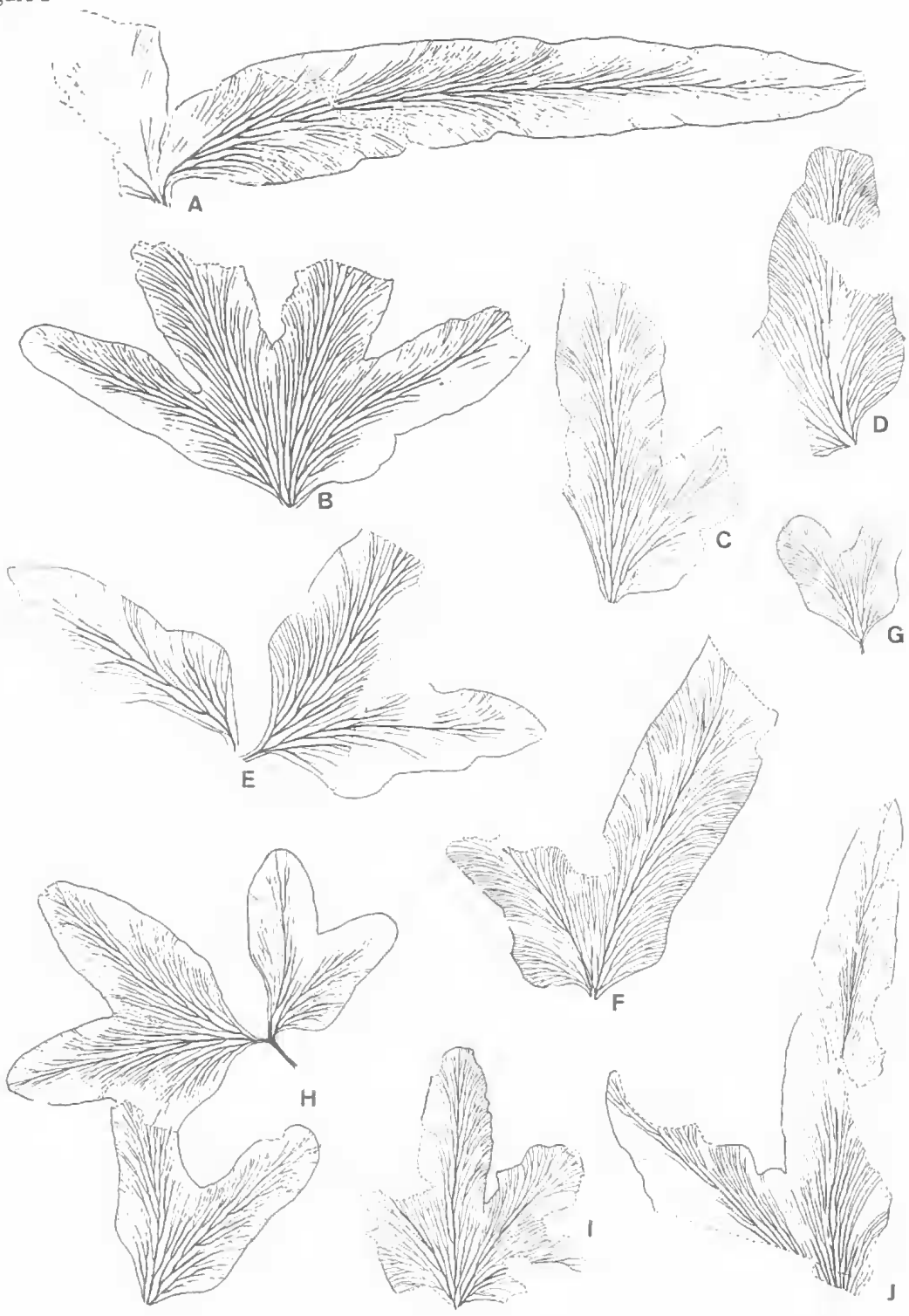


Figure 6

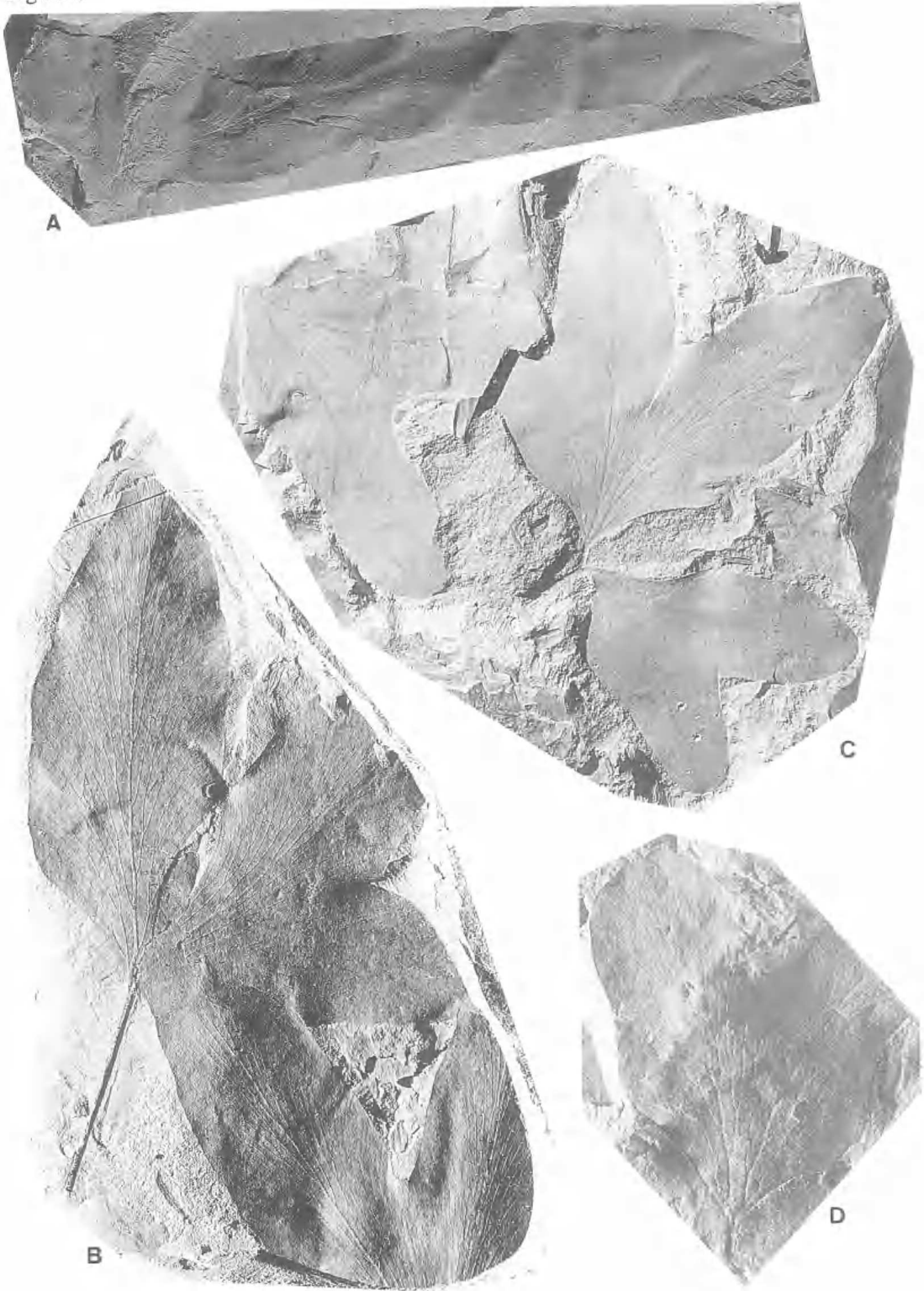


Figure 7

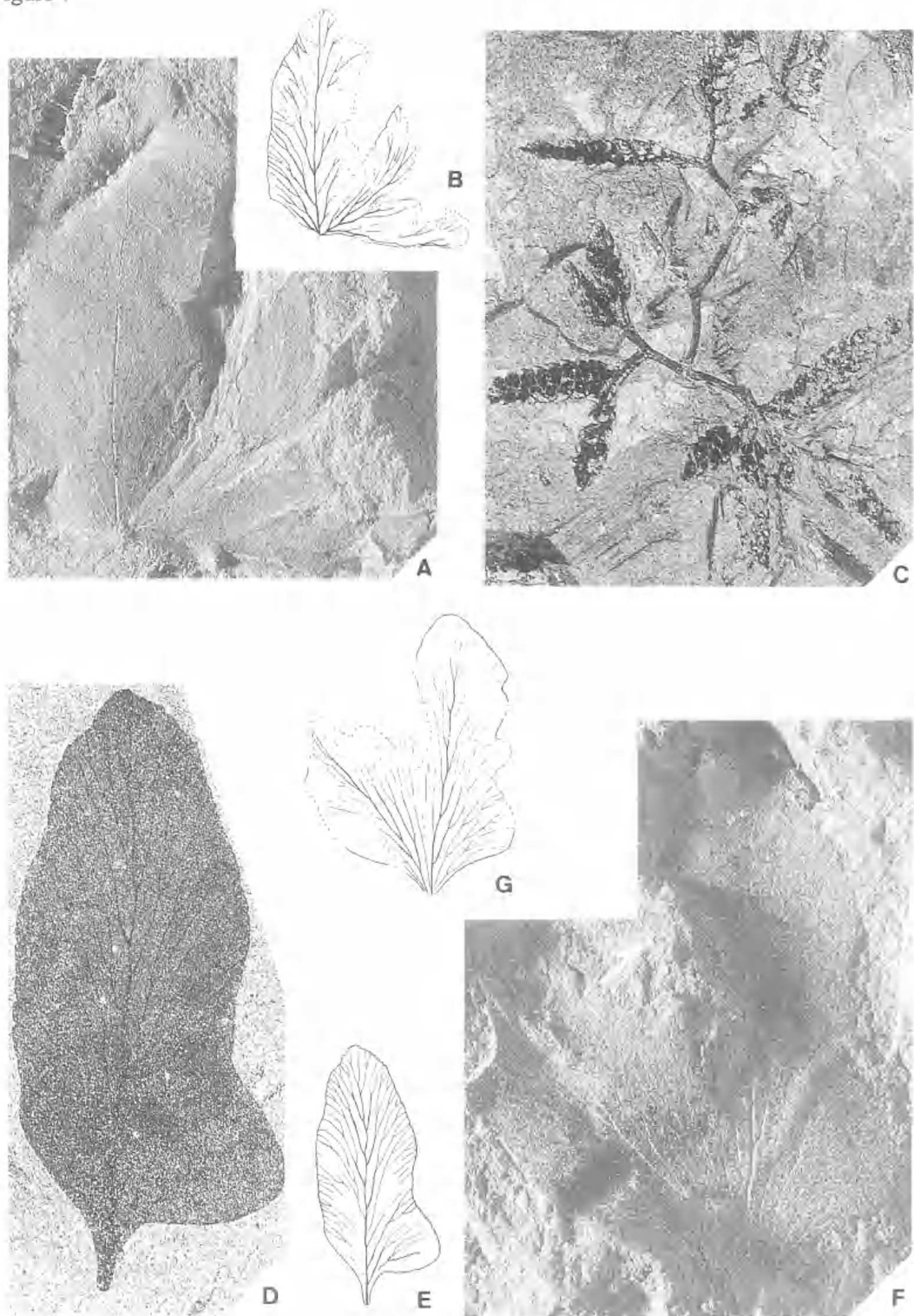


Figure 8

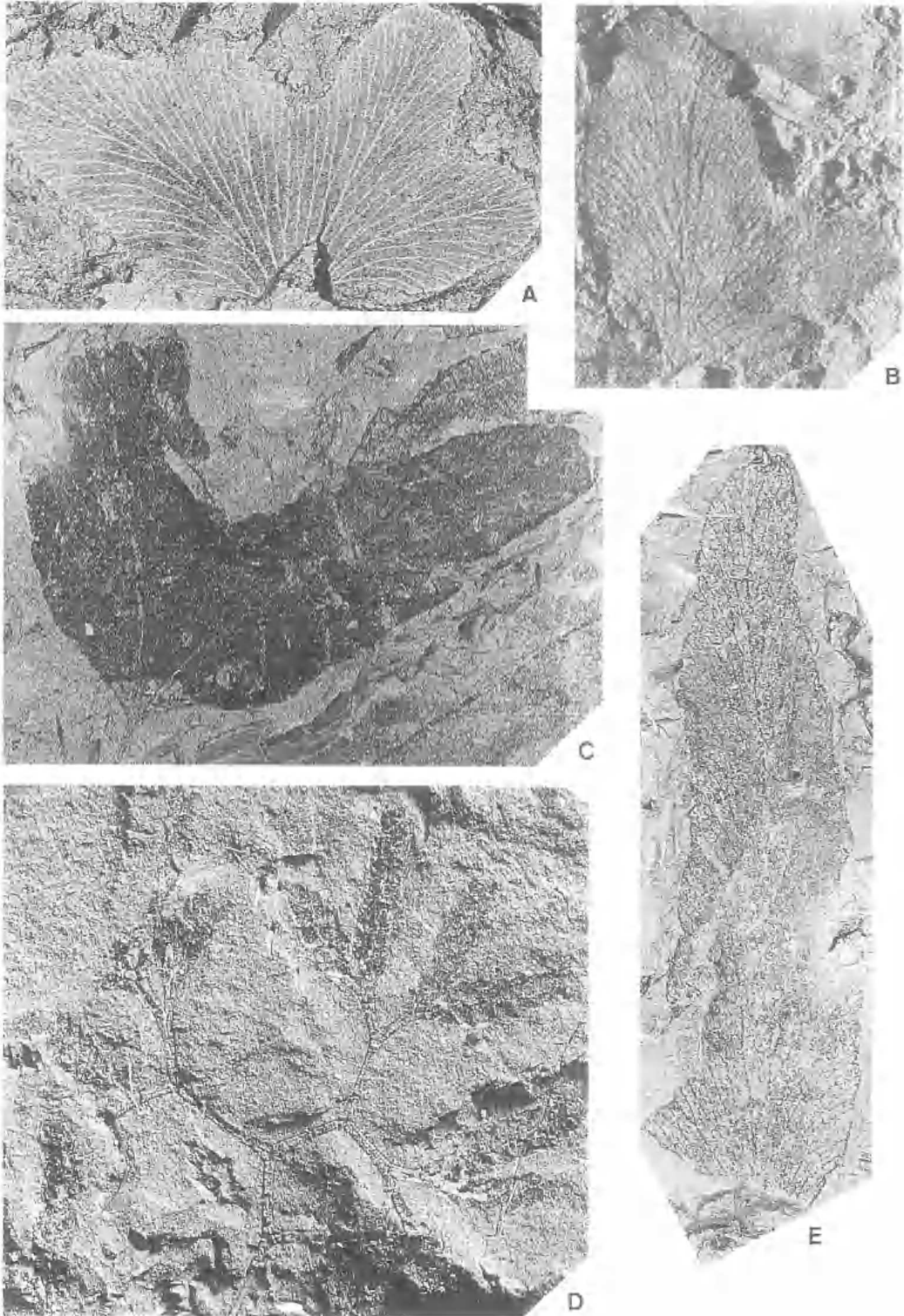


Figure 9

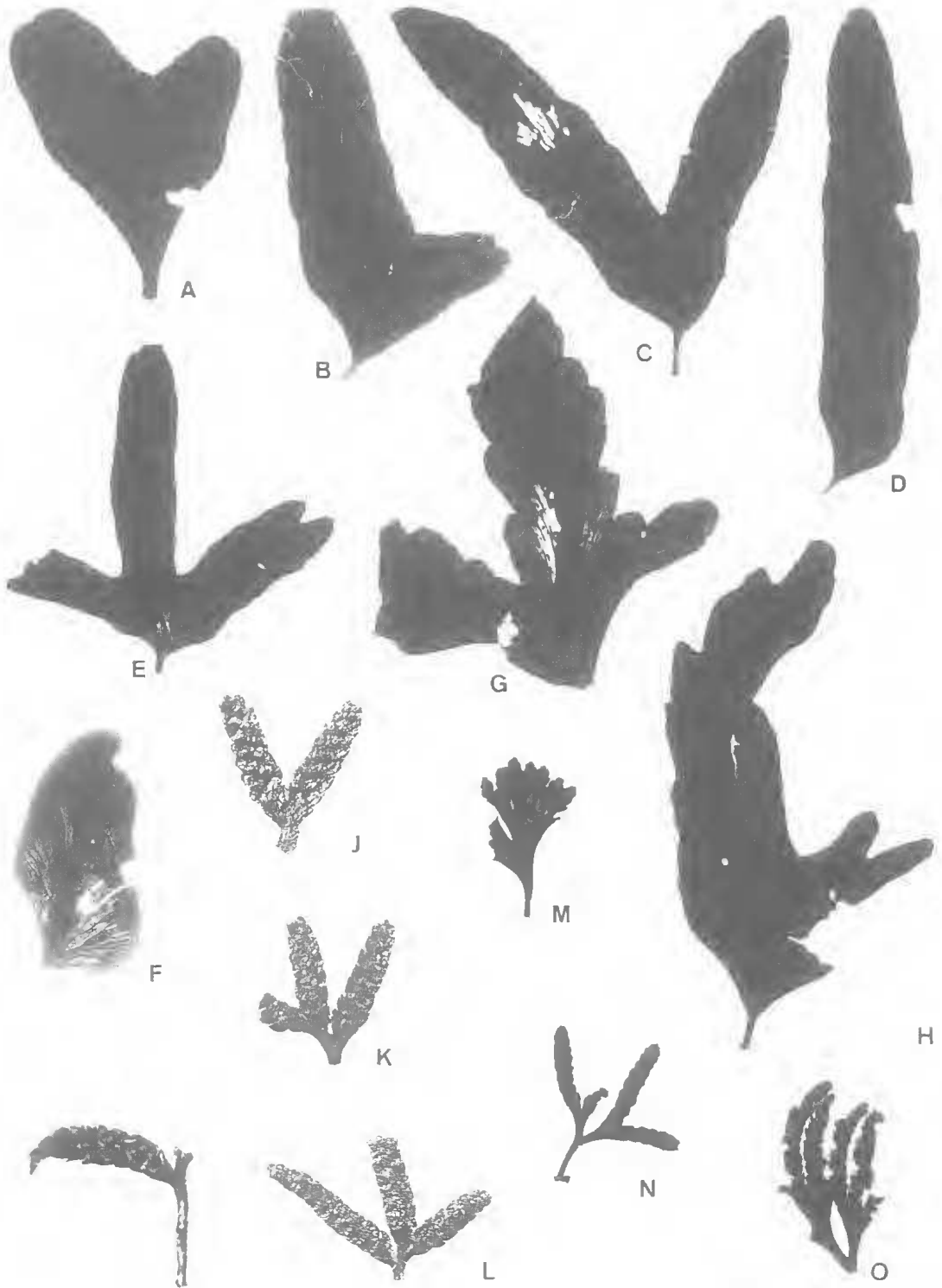


Figure 10

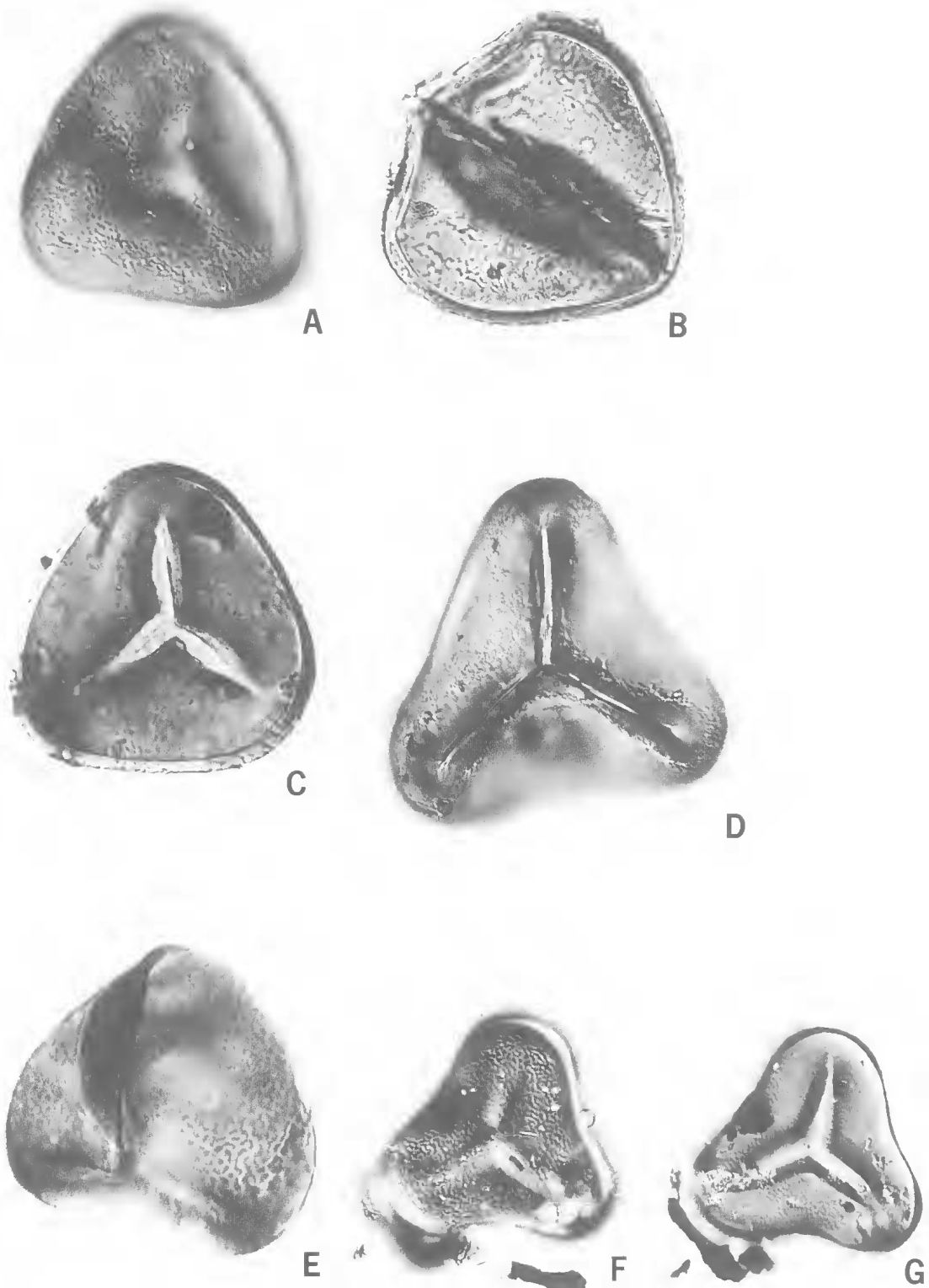
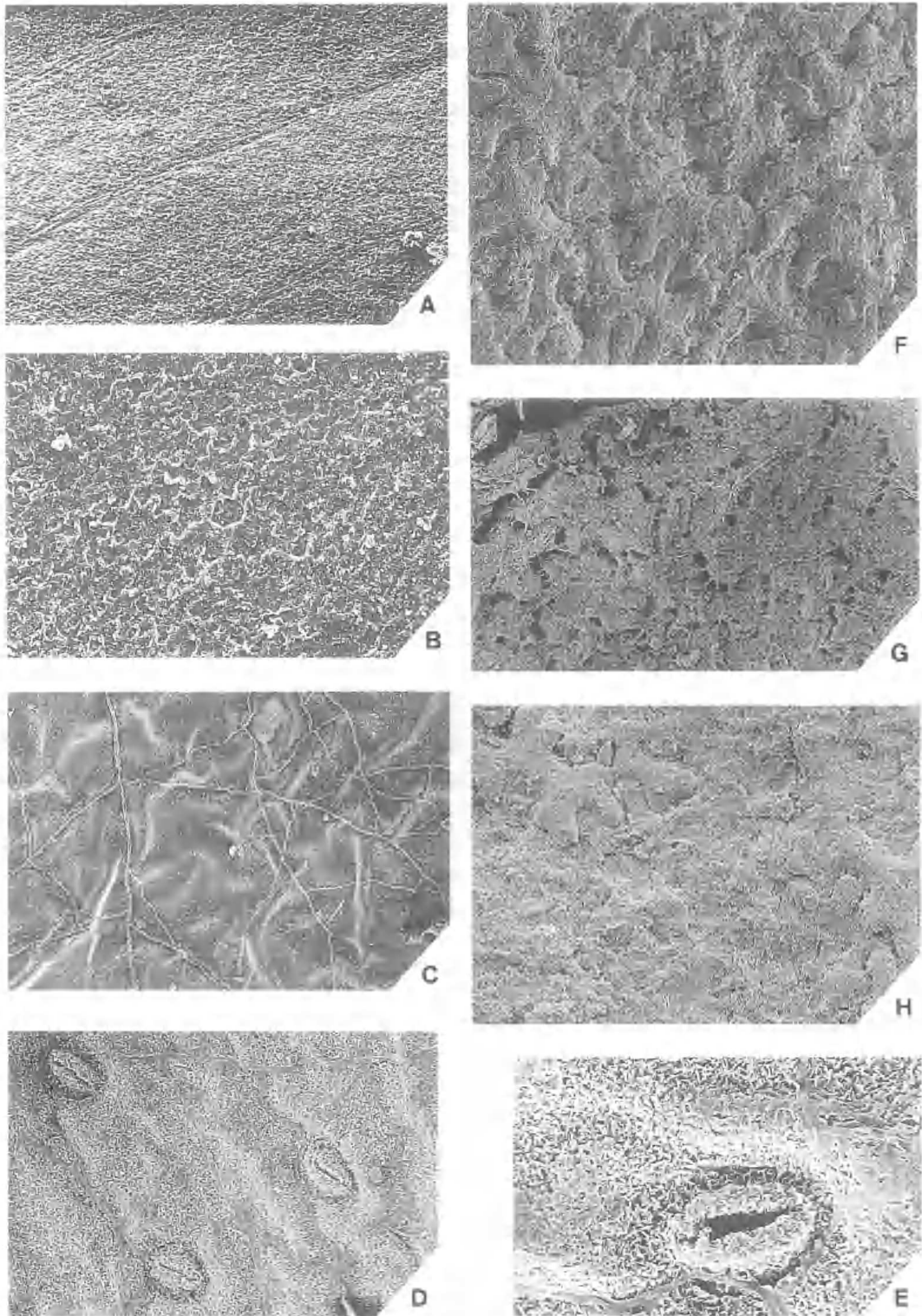


Figure 11



height above ground and perhaps polyploidy and hybridization that even with ample material it is not easy to give specific limits'. Fossil *Lygodium* presents further problems due to the incomplete and fragmentary material available for study. The overlap in morphology and variation in sterile *Lygodium* pinnules from sites in Australia and New Zealand is presented in Table 1. As Dinmore and Golden Grove have yielded the largest amount of vegetative and fertile material, discussion centres on material from these two localities. The strongly dimorphic sterile and fertile pinnules occur in association at Dinmore, Golden Grove, Anglesea and Maslin Bay. Material from Dinmore indicates that the sterile and fertile *Lygodium* pinnules can be referred to the same plant (Fig. 4E-F).

STERILE PINNULE MORPHOLOGY

Fossil *Lygodium* pinnules from the various sites are asymmetrical and palmately lobed. The number of lobes in sterile *Lygodium* was used by Berry (1930) to define new fossil taxa, although it is an extremely variable feature. *Lygodium* pinnules at most sites, but particularly at Dinmore and Golden

Grove, exhibit considerable variation in the number and degree of lobation (Table 1). At Dinmore, unilobate and trilobate and bilobate and trilobate pinnules have been found in organic connection (Figs 5E,H,6C). In the extant New Zealand species *L. articulatum*, unilobate pinnules predominate but fused bilobate pinnules occur. Similarly, in fossil *Lygodium* from Dinmore, bilobate and trilobate pinnules are the most common, although rare quadrilobate and pentalobate pinnules occur (Fig. 5B,I). These are interpreted as resulting from the fusion of trilobate with unilobate and bilobate pinnules. Bilobate and trilobate pinnules also predominate in the Golden Grove, and Maslin Bay localities (Table 1). The Australian fossil *Lygodium* pinnules resemble extant *L. palmatum* in having multilobate pinnules but like *L. kaulfussii* Heer, they differ in their larger, more elongate pinnules.

All the major localities in Australia have yielded sterile pinnules with petiolules. In most specimens the petiolules are short (<3.0mm long), except a few specimens from Dinmore which have a preserved petiolule length of up to 15.0 mm (Fig.

FIG. 8. Sterile and fertile *Lygodium dimorphophyllum* from Anglesea. A, Quadrilobate sterile pinnule, NMVP178150, $\times 2.3$. B, Bilobate sterile pinnule, NMVP178148, $\times 2$. C, Bilobate sterile pinnule, NMVP178149, $\times 2.2$. D, Sorophore, arrow indicates prominent obtuse branching of sorophore, NMVP165681, $\times 4.6$. E, Fragmentary single lobe of large sterile pinnule, NMVP178145, $\times 2$. [Photographs of NMVP165681 provided by J. Douglas].

FIG. 9. Sterile and fertile *Lygodium dimorphophyllum* from Golden Grove. A-H, Sterile pinnules. A, Small pinnule, UAG3024, $\times 2.5$. B, Bilobate pinnule, UAG3022, $\times 1.5$. C, Bilobate pinnule, UAG2604, $\times 1.6$. D, Unilobate pinnule, UAG3004, $\times 1.2$. E, Trilobate pinnule, UAG1379, $\times 1.2$. F, Small unilobate pinnule, UAG3003, $\times 1$. G, Aberrant trilobate pinnule with multiple accessory lobing, UAG2718, $\times 1.7$. H, Aberrant bilobate pinnule with multiple accessory lobes, UAG3018, $\times 1.5$. I-O, Terminal sorophores, all $\times 4$. I, UAG3037. J, UAG3036. K, UAG3039. L, UAG3038. M, UAG3042, $\times 1.7$. N, UAG3040, $\times 1.7$. O, UAG3041, $\times 1.5$.

FIG. 10. Spores macerated from *Lygodium dimorphophyllum* sporophores from Golden Grove and Anglesea; and late Paleocene *Cyathidites splendens* from the Lake Eyre Basin. A, Ornamentation of distal surface of *L. dimorphophyllum* spore, Golden Grove. Original magnification $\times 40$. Zeiss location 20.8/87.4; England FINDER Location V 17/0. B, Equatorial view of *L. dimorphophyllum* spore, Golden Grove, showing thickened exine and reduced ornamentation. Original magnification $\times 40$. Zeiss location 19.6/99.0; England FINDER Location U 29/0. C, Proximal view of *L. dimorphophyllum* spore, Golden Grove, showing slightly thickened radials and gaping laesura. Original magnification $\times 40$. Zeiss location 19.6/122.5; England FINDER Location U 53/0. D, Proximal view of *L. dimorphophyllum* spore, Golden Grove, showing thickened labra and reduced ornamentation. Original magnification $\times 40$. Zeiss location 14.8/101.3; England FINDER Location P 31/0. E, Oblique equatorial view of *L. dimorphophyllum* spore, Anglesea, PB5304, with strongly developed rugulate ornamentation. Original magnification, $\times 40$. Zeiss location 18.8/104.9; England FINDER Location T 35/0. F, Distal surface of *C. splendens*. Muloorina 2 well, 34 metres depth, showing rugulate and verrucate ornamentation. Original magnification $\times 16$. Zeiss location 10.5/95.8; England FINDER Location L 26/1. G, Proximal surface of same specimen with reduced ornamentation, gaping laesura and slightly thickened radials.

FIG. 11. SEM of fossil and modern *Lygodium* cuticle. A, B, Anticlinal walls of epidermis in sterile *L. dimorphophyllum* pinnules from Dinmore, QMF18904. A, Venation and general appearance of leaf impression, note venation $\times 50$. B, Sinuous anticlinal walls of epidermis $\times 140$. C, SEM of adaxial surface of *L. articulatum* cuticle, showing wax covered cuticle and fungal hyphae, $\times 270$. D, E, SEM of abaxial surface of *L. articulatum* cuticle. D, showing arrangement of stomata $\times 260$. E, Detail of stomata $\times 700$. F-H, Cuticle from *L. dimorphophyllum* leaves and sorophores from Golden Grove. F, Abaxial surface, showing arrangement of stomata, UAG3021, $\times 320$. G, Cuticle from fertile sorophore of UAG3041, $\times 430$. H, Adaxial surface of leaf cuticle, UAG3021, $\times 350$. [Photographs of Figs 11A,B supplied by M.E. Detmann and H.T. Clifford].

TABLE 1. Comparison of the morphology of sterile *Lygodium* pinnules from localities in Australia and New Zealand.

| LOCALITY | PINNULE SHAPE | VENATION | PINNULE APEX | PINNULE BASE | REFERENCES |
|---|---|-------------|-----------------------|--------------------------|------------------------------------|
| <i>L. dinmorphyllum</i> | | | | | |
| Dinmore, Queensland | asymmetrical/palmate; bi., tri., quad., pentalobate | dichotomous | acute, obtuse, retuse | cuneate, truncate | Churchill, 1969; Hill et al., 1970 |
| Anglesea, Victoria | asymmetrical/palmate; bilobate, quadrilobate | dichotomous | acute, obtuse, retuse | cuneate | Douglas, 1978 |
| Maslin Bay, S. Aust | asymmetrical/palmate; uni., bi., trilobate | dichotomous | acute, obtuse | cuneate, truncate | — |
| Golden Grove, S. Aust | asymmetrical/palmate; uni., bi., trilobate | dichotomous | acute, obtuse, retuse | cuneate, truncate | Christophel and Greenwood, 1987 |
| <i>Lygodium</i> sp. | | | | | |
| Cethana, Tasmania | asymmetrical/palmate?; uni., bilobate | dichotomous | acute?, obtuse | cuneate | — |
| Temuka, New Zealand | asymmetrical/palmate?; uni., trilobate | dichotomous | obtuse, acute | truncate | |
| Vegetable Creek, N.S.W (<i>L. strzeleckii</i>) | unilobate | dichotomous | obtuse | — | Ettingshausen, 1886 |
| <i>L. skottsbergii</i> | | | | | |
| Chile (fossil) | asymmetrical/palmate; bi., trilobate | dichotomous | acute, obtuse | truncate, broad, cuneate | Halle, 1940 |
| <i>L. articulatum</i> | | | | | |
| New Zealand (extant) | usually unilobate, rarely bilobate | dichotomous | acute | cuneate | |

6B). The end of the petiolule in the Golden Grove material is frequently enlarged indicating a point of attachment and probably also dehiscence (Fig. 9B-E,H). In extant *L. articulatum*, sterile and fertile pinnules lack a petiolule, and the abscission node occurs at the leaf base (Fig. 2). This feature also occurs in the fossil *L. kaulfussi* and was used by Manchester and Zavada (1987) to differentiate between *L. kaulfussi* and *L. skottsbergii*. *Lygodium skottsbergii* and the fossil Australian material resemble extant *L. palmatum* in that their leaflets are firmly affixed to short petiolules (Manchester & Zavada, 1987).

The pinnule margins in *L. dinmorphyllum* are entire to undulose with some specimens showing irregular lobation (Fig. 9G,H). One of the Cethana specimens (Fig. 3B) is irregularly serrate and is tentatively referred to *Lygodium*. The serration is accentuated by tearing of the leaf lamina and margins during fossilization. The other specimen is asymmetrical and bilobate (Fig. 3C) and comparable to other *Lygodium* material. The concavely curved basal margin of the pinnule is similar in both specimens. This feature occurs consistently

in most of the Tertiary *Lygodium* material in Australia. The base of the pinnule is typically cuneate or truncate while in *L. kaulfussi* it is rounded to obtuse or cordate (Manchester & Zavada, 1987).

The venation in the fossil Australian and New Zealand material is dichotomous, branching 2-3 times before reaching the margin. The venation of the Australian *Lygodium* material appears indistinguishable from *L. kaulfussi* from the Eocene material from Wyoming figured by Manchester & Zavada (1987). Dichotomous venation is typical of most *Lygodium* species except those with reticulate venation, e.g. *L. reticulatum*.

Preservation of the mode of branching and evidence of the climbing habit which is characteristic of modern species in this genus is rare in the fossil record and is unlikely to occur in those species whose pinnules dehisce at senescence. The only evidence of the mode of branching in fossil *Lygodium* comes from impressions at Dinmore.

FERTILE PINNULE MORPHOLOGY

The sorophores of *L. dinmorphyllum*, like those

of *L. kaulfussi* and the extant species *L. palmatum* and *L. articulatum*, are produced terminally on branched axes. The sorophores vary in size, reflecting their position on the plant and stage of development. *Lygodium skottsbergii*, *L. articulatum* and *L. dinmorphyllum* all show variation in reduction of lamina in fertile pinnae. The fertile pinnae of *L. articulatum* vary in the free lamina between sorophores (Fig. 2) and *L. skottsbergii* shows similar variation in the amount of leaf lamina between sorophores (Halle, 1940: pl. 1, figs 4-8). *Lygodium dinmorphyllum* pinnae from Dinmore exhibit similar ranges of variation (Fig. 4) with some fertile pinnae 'free' of lamina, and others bearing extensive laminae between the sorophores (Churchill, 1969: fig. 2). In most of the Golden Grove, Maslin Bay and Anglesea material the fertile pinnae are nonlaminar. Fertile pinnae of *L. kaulfussi* are also nonlaminar although pinnules intermediate in character between sterile and fertile pinnules are preserved (Manchester & Zavada, 1987: fig. 8). The sorophores attached to the sterile pinnule from Dinmore can similarly be explained as a 'leaflet' intermediate in character between sterile and fertile pinnules (Fig. 4E-F). The annulus on the sporangia is not preserved in material from any site. Halle (1940) and Manchester & Zavada (1987) noted that the annulus could not be discerned in *L. skottsbergii* and *L. kaulfussi* respectively.

SPORE MORPHOLOGY

Spores from complete sorophores of *L. dinmorphyllum* are known from Anglesea (Douglas, 1978) and have been extracted from Golden Grove material. The spores broadly resemble those from fossil *Lygodium* (excluding *L. poolensis* Chandler, 1955) described from the Northern Hemisphere (Buzek & Konzalová, 1983; Chandler, 1955; Manchester & Zavada, 1987). Although spores were recovered from *L. dinmorphyllum* from a number of sites the best preservation is in the Golden Grove material and descriptions are based on this material. In general, the spores possess a subtriangular amb with convex to straight (occasionally concave) interradials and rounded radials. The laesura are slightly sinuous, often open and gaping, and extend two thirds of spore radius towards the amb. The laesura are bordered by labra 5-7 µm wide and raised 6-8 µm. Spore exine is approximately 2 µm thick and thickened in the radial areas to 5 µm. Ornamentation is best developed on the distal surface and comprises low verruca, short rugula and low sinuous to bifurcating ridges enclosing short ir-

regular lumina; ornamentation is reduced on the proximal surface, particularly in the proximal polar area (Fig. 10). In optical section the amb is gently undulating. Some specimens appear to bear remnants of an irregular perisporium. Based upon measurements from 15 specimens the equatorial diameter of the spores is 67 (82) 95 µm and polar diameter is 59 (75) 90 µm.

The spores from *L. dinmorphyllum* sorophores are identical to the form species *Cyathidites splendens* Harris, 1965. The holotype of *C. splendens* was examined but the mounting medium and spore are too dehydrated to provide useful morphological information and comparisons were limited to photographs and published descriptions. However free spores of *C. splendens* occur consistently in the Golden Grove and Maslin Bay carbonaceous lenses as well as other Australian early Tertiary sediments (Fig. 10). *Cyathidites splendens* has also recently been recognized in Late Cretaceous (Maastrichtian) sediments from the offshore Bight and Duntroon Basins, off South and Western Australia (NA, pers. obs). Spores of the form species *C. gigantis* (Cookson) Harris, 1965 also bear some similarity to the spores extracted from the *L. dinmorphyllum* sorophores. However the holotype of *C. gigantis* and other free spores from early Tertiary sediments were examined and found to be smaller, possess a much thickened exine with prominently thickened radials, and coarse ornamentation in the proximal polar area, diminishing greatly in the equatorial interradial areas. The *L. dinmorphyllum* spores therefore correlate with the form species *C. splendens* Harris, 1965.

CUTICLE MORPHOLOGY

Attempts to prepare cuticle from the mummified Golden Grove leaves have proved difficult but small fragments were obtained. *Lygodium dinmorphyllum* pinnules from Golden Grove are probably hypostomatic as is modern *L. articulatum*. The stomata of *L. dinmorphyllum* from Golden Grove are anomocytic, as in extant *Lygodium* (Clifford & Constantine, 1980) and the anticlinal epidermal walls are strongly sinuous (Fig. 11 F,H). The stomata appear to be irregularly oriented on the leaf surface as in modern *L. articulatum* (Fig. 11D). SEM micrographs of impressions of Dinmore material also demonstrate sinuous anticlinal epidermal walls but stomata are not evident (Fig. 11 A,B). *Lygodium kaulfussi* has sinuous anticlinal epidermal walls and stomata comparable in size to those of *L. dinmorphyllum*. Unlike *L. dinmorphyllum* the stomata in *L. kaul-*

fussi are diacytic, arranged in rows and the anticlinal epidermal walls are not as strongly sinuous (Kräusel & Weyland, 1950). The stomata in *L. kaulfussi* are oriented between two epidermal cells, while in *L. dinmorphyllum* the stomata are surrounded by four or five cells.

The cuticle of *L. dinmorphyllum* sorophores indicates that the anticlinal epidermal walls are sinuous but not to the same extent as the leaves (Fig. 11G). No stomata were seen.

CONCLUSION

Even with ample material as provided by the Golden Grove and Dinmore localities, species assessment is difficult, as the material is extremely variable. The limited material from Cethana or Temuka is therefore difficult to interpret particularly with only photographic evidence available. Similarly early records of *Lygodium* (such as Ettingshausen, 1886, 1888), which are based solely on sterile foliage are also not presently resolvable. Northern Hemisphere species based on limited material present similar problems as Manchester & Zavada (1987) have shown.

Palaeobiogeographical speculation on the radiation and evolution of *Lygodium* is difficult because of the cosmopolitan distribution and extensive Tertiary fossil record (Kräusel & Weyland, 1950; Reed, 1947). The extensive fossil record of *Lygodium* in Australia suggests that the extant Australian species may be derived from these early Tertiary forms. However, as fossil *Lygodium* is also known from the Miocene Notonakajima flora of Japan and Oligocene floras of Manchuria (Matsuo, 1963; Florin, 1922) it is equally possible that the modern northern Australian species *L. japonicum*, *L. flexuosum*, *L. microphyllum* and *L. reticulatum* are recent arrivals from Asia as Page & Clifford (1981) speculated. These species are all widely distributed within the Malesian region (Holtum, 1959). The weakly dimorphic fertile foliage of most of the Malesian species, i.e. the fertile pinnules resemble the sterile pinnules, suggests a closer affinity to *L. mioscandens* Matsuo (1963) from Japan than with the fossil material from the early Tertiary of Australia. Manchester & Zavada (1987) suggested that species with lamina surrounding the sorophores, e.g. *L. japonicum* and *L. flexuosum* are relatively recent in origin. The high diversity of *Lygodium* species in the Malesian area may be due to a relatively recent and rapid speciation and radiation in this region. This may explain, in part,

Holtum's (1959: 39) difficulties in defining modern species within the genus.

Cyathidites splendens ranges from the Late Cretaceous through to the Pliocene in southern Australia. In the early Tertiary Eyre Formation of the Lake Eyre Basin *C. splendens* is common and can be locally more frequent in parts of the Paleocene section. The frequency of the spore in palynomorph assemblages, however, decreases through the Tertiary and *C. splendens* is rare in Pliocene assemblages. *Cyathidites splendens* is commonly associated with palynofloral assemblages that are indicative of rainforest communities. The gradual decrease in the frequency of *C. splendens* through the Tertiary in southern Australia may be related to the overall decline in temperature and precipitation during this interval.

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- UQF10726 (S); UQF12450-1 (F); UQF32006 (S).
GSQF12973 (F); GSQF12974 (S); NMVP26688 (F)
Holotype, *L. dinmorphyllum*; NMVP26689 (F)
Paratype, *L. dinmorphyllum*.
- Cethana, Tasmania
UTC232 (S); UTC235 (S).
- Vegetable Creek, N.S.W.
GNSWF8820 (S), Holotype, *L. strzeleckii*.
- Maslin Bay, North Maslin Sands, S.A.
UAS715-6 (S); UAS1211 (S); UAS1868 (S);
UAS2274 (S); UAS2513-4 (S); UAS2691-2 (S);
UAS3502 (S); UAS3524 (F); UAS3537-8 (S);
UAS3546-7 (S).

APPENDIX A

LYGODIUM MATERIAL EXAMINED (F=fertile. S=sterile)

- Dinmore, Redbank Plains Formation, SE Qld
QMF2857-8 (S); QMF12544 (F); QMF13464 (S);
QMF14096 (S); QMF14360 (S); QMF14361 (S/F);
QMF14362-3 (S); QMF14365-7 (S); QMF14464-7 (F);
QMF14530 (F); QMF15809 (S); QMF14924 (F);
QMF14974 (S); QMF15314 (S); QMF15317 (F);
QMF15318-9 (S); QMF15320-1 (S); QMF18035 (S);
QMF18904 (S). UQF10620 (F); UQF10720 (F);
- Golden Grove, North Maslin Sands, S.A.
UAG1379 (S); UAG1398 (S); UAG1400 (S);
UAG2604-5 (S); UAG2607-8 (S); UAG2718 (S);
UAG2720 (S); UAG3001-26(S); UAG3036-42 (F).
- Anglesea, Eastern View Coal Measures, Victoria
NMVP165681 (F); NMVP178144-9 (S);
NMVP178150 (F).
- Temuka, New Zealand
NZGSB25/90-92.